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Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie

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Abstract. Fires in the tallgrass prairie are frequent and significantly alter nutrient cycling processes. We evaluated the short-term changes in plant production and microbial activity due to fire and the long-term consequences of annual burning on soil organic matter (SOM), plant production, and nutrient cycling using a combination of field, laboratory, and modeling studies. In the short-term, fire in the tallgrass prairie enhances microbial activity, increases both above- and belowground plant production, and increases nitrogen use efficiency (NUE). However, repeated annual burning results in greater inputs of lower quality plant residues causing a significant reduction in soil organic N, lower microbial biomass, lower N availability, and higher C:N ratios in SOM. Changes in amount and quality of belowground inputs increased N immobilization and resulted in no net increases in N availability with burning. This response occurred rapidly (e.g., within two years) and persisted during 50 years of annual burning. Plant production at a long-term burned site was not adversely affected due to shifts in plant NUE and carbon allocation. Modeling results indicate that the tallgrass ecosystem responds to the combined changes in plant resource allocation and NUE. No single factor dominates the impact of fire on tallgrass plant production.

Introduction

Aboveground plant production in mesic grasslands generally increases following a fire. These increases in plant production have been attributed to improved microclimatic conditions, removal of nutrient-immobilizing plant debris, release of readily available nitrogen, phosphorus, and cations, and enhanced N fixation (Daubenmire 1968; Hulbert 1969; Old 1969; Rice & Parenti 1978; Woodmansee & Wallach 1981; Knapp & Seastedt 1986). Most discussions of fire effects on grasslands have focused on the immediate system responses to fire, which include changes in soil temperature, light, moisture, and nutrients (Kucera & Ehrenreich 1962; Anderson 1965; Owensby & Anderson 1967; Anderson et al. 1970; Hobbs & Schimel 1984). Repeated annual burning has cumulative long-term effects on ecosystem properties, such as lower levels of soil organic matter, altered species composition, and modified carbon allocation patterns of plants (Daubenmire 1968; Launchbaugh & Owensby 1978; Biederbeck et al. 1980; Risser & Parton 1982; Towne & Owensby 1984). The mechanisms by which the short-term or immediate effects of burning are translated into the long-term behavior of a tallgrass ecosystem with regular annual burning are not well understood.

The absence of fire in the tallgrass prairie results in an accumulation of litter. The build up of litter lowers soil temperatures (Hulbert 1969; Old 1969; Rice & Parenti 1978) and acts as a filter for atmospheric inputs of nutrients (Knapp & Seastedt 1986). The large litter accumulation (10–30 cm depth) in unburned tallgrass prairie also reduces light near the soil surface so that maximal photosynthetic rates are reduced (Knapp 1984, 1985; Schimel et al. 1991). Prolonged absence of fire in the tallgrass prairie causes changes in species composition and the invasion of woody species (Hadley & Kieckhefer 1963; Old 1969; Vogl 1974; Bragg & Hulbert 1976; Kucera 1981).

Ecosystem responses to fire involve a complex set of interactions that begin with the removal of aboveground plant biomass, resulting in reduced inputs of C and N into the soil system. Nitrogen mineralization from soil organic matter (SOM) is enhanced due to elevated soil temperatures. Mineralization of SOM occurs earlier in the growing season, resulting in greater nutrient availability. Nitrogen availability also increases due to non-symbiotic N fixing bacteria that respond to elevated levels of available P in the post-burn ash (Eisele et al. 1990). Plant growth, overall, is enhanced as a consequence of earlier "green-up" and by greater N availability. Losses of N occur primarily during combustion rather than by leaching or denitrification pathways (Seastedt & Ramundo 1990). Further, fire changes nitrogen use efficiency (NUE defined as grams C produced per g N utilized) and root-to-shoot allocation.

We had two objectives; the first was to determine the short-term effects of burning on nutrient cycling and plant production. The second was to determine the cumulative effect of annual burning on the long-term dynamics of soil organic matter, plant production, net N mineralization rates, and microbial biomass. This latter objective was also addressed by using the CENTURY model (Parton et al. 1987) to test the integrated impact of fire on the tallgrass ecosystem.

Methods

Study area

Field sites were located in the Flint Hills near Manhattan, KS. This region is one of the few remaining unplowed areas of extensive tallgrass prairie. The Flint Hills are located along the western border of the tallgrass province and extend in a north-south direction from near the Nebraska-Kansas border into

Oklahoma. They form roughly a 70-km wide band of rolling hills composed of hard cherty and flinty Permian limestone. The steep and rocky topography make the Flint Hills unsuitable for conventional farming, so the region is used primarily for cattle ranching and has been grazed with cattle since the late 1800s. The vegetation is dominated by *Andropogon gerardii* Vittm., *Sorgastrum nutans* (Michx.) Nash, and *Panicum virgatum* L., species typical of the tallgrass prairie in eastern Kansas.

Two currently ungrazed sites were used for this study – Aldous and Konza plots. The Aldous plots were established on moderately grazed and burned pasture in the late 1920s to study the effect of burning at different times of the year (Aldous 1934; Towne & Owensby 1984). In this study, the late spring burn and the unburned treatments of the Aldous study were used to investigate the long-term effects of annual burning. Soil at the Aldous site is mainly loess-derived Smolan silt loam, classified as a Pachic Argiustoll. The Konza plots were located on the 3487-ha Konza Prairie Research Natural Area (KPRNA), a Long-Term Ecological Research (LTER) site approximately 12 km southwest of Manhattan, KS. Approximately 90% of the KPRNA is unplowed tallgrass prairie, most of which has been under good to excellent grazing management during the past 100 years and burned three out every four years until 1971 (Dokken & Hulbert 1978). Konza plots were used to investigate short-term responses to burning on plots that were ungrazed and unburned since 1971 until the time of this study (i.e., 1983 and 1984). The plots were located on a relatively flat bench of a north-facing hillside, with depth to limestone rock of approximately 70 cm. The soil is Clime clay loam, classified as a Udic Haplustol.

At both sites, the experimental design consisted of two plots of each burn and unburned treatments. The size of the Aldous plots was 20 m by 10 m with 0.5-m buffer strips; samples were taken at least 1 m from the edge of a plot boundary. The size of the Konza plots was 7 m by 7 m with 1-m buffer strips. Samples were taken from the inner 5 m by 5 m area of each plot. The plots were burned during the last week in April at both sites. The burning was initiated with a slow burning backing fire at one corner of the experimental plot. Once the backing fire burned partially into the plot, a head fire was lit to consume the remaining portion of the plot (usually 75% of a plot was burned by the head fire).

Above- and Belowground Plant C and N

Above- and belowground plant biomass C and N were measured in late August of 1984 (time of peak root and shoot biomass) at Konza after two successive years of burning. At Aldous, only belowground plant C and N were measured, in late August 1984. Aboveground biomass measurements were made using ten 0.1-m^2 rectangular plots per treatment. Aboveground plant parts were clipped, separated into live, standing dead (current season dead), and litter (past season dead) categories, oven-dried at 60 °C, and weighed. Few forb or shrub species were found on the site, and only graminoid data will be presented here.

Roots were sampled using ten 5-cm diameter soil cores taken to 30-cm depth per treatment. The roots were washed from the soil, and the material rinsed into a 60-mesh sieve. Live and dead roots were separated by visual inspection (Hayes & Seastedt 1987). Root material was dried at 60 °C and subsamples were ashed in a muffle furnace at 475 °C. Values for all plant components are expressed in units of kg/ha ± 95% CI.

Soil analyses

Soil temperature was measured at 2 cm depth in burned and an unburned plot at Konza using a OMNIDATA thermistor. Soil moisture was measured gravimeterically from the top 5 cm at all plots using a subsample of the microbial biomass soil samples. The effect of fire on soil nutrient levels and availability was determined by measuring soil organic C and N, NO_3^- and NH_4^+, belowground net N mineralization rates, and soil microbial C and N for burned and unburned plots at Aldous and Konza. Soils were collected from the 0–5 cm and 5–15 cm depth increments. Ten samples were collected from each treatment. Total carbon was determined by wet oxidation (Snyder & Trofymow 1984). Inorganic N ($NH_4^+ + NO_3^- + NO_2^-$) was determined using a Technicon Autoanalyzer I (Technicon Industrial Systems, Tarrytown, NY). Total N determinations were made with a micro-Kjeldahl procedure (Nelson & Sommers 1980).

Field Mineralization Study

Nitrogen mineralization rates were determined in the field using the buried bag technique (Eno 1960; Westerman & Crothers 1981). Mineralization rates were measured by the difference in inorganic N concentrations in an initial soil sample and in a soil maintained in a buried bag for a 30-d incubation in the field. We used reciprocal transplants of buried bags to determine the effects of differences in soil temperature between treatments (e.g., burn vs unburned) on mineralization rates after fire. Soils in buried bags from burned plots were transferred to unburned plots and, similarly, unburned soils were transferred into burned plots. These samples are referred to as "Transfer Bags" in contrast to "In situ Bags," which were incubated in the plots from which the soil was collected. Comparisons between the In situ and Transfer bags show the effects of post-fire soil temperature changes on N mineralization while maintaining similar soil characteristics (soil organic C and N content, soil moisture, pH, etc.).

Incubations and microbial biomass determinations

Soil samples were collected monthly during the growing season and returned to the laboratory. All samples were processed within 48 hrs. Soils were wet sieved through a 2-mm sieve to remove large roots and rocks. Soil moisture determinations and initial NH_4^+ and $NO_2^- + NO_3^-$ concentrations were determined on replicated subsamples. Microbial biomass was measured following Jenkinson & Powlson (1976) as modified by Schimel et al. (1985). For each soil sample, paired $CHCl_3$ fumigated and non-fumigated subsamples were incubated at field capacity and 25 °C in the dark. The non-fumigated samples were extracted for inorganic N at 10 and 20 d in 1983 and after 10, 20, and 70 d in 1984. Soil respiration (Cr) from these samples was also measured on the non-fumigated soil samples (Schimel et al. 1985). Microbial biomass C and N were calculated following Jenkinson & Powlson (1976 a, b) as modified by Voroney (1983), Horton (1985), and Schimel et al. (1985).

Model Simulation of Fire Impacts

We used the CENTURY model (Parton et al. 1987; Ojima et al. 1990) to examine the effects of burning on three general processes and their interactions in tallgrass prairie. Modifications were based on observed data from the Konza prairie and the Aldous plots. First, we modified biological N inputs by calculating biological N_2 fixation rates as a function of the ratio of mineral N to labile P (high C_2H_4 reduced to N fixed. Secondly, we incorporated the combustion losses of aboveground C, N and P into the model based on field observations reported here. Third, we modified plant physiological parameters by increasing the root:shoot ratio (R:S) from 1.1 to 1.5 and by increasing the C:N ratio (C:N) of plant tissues following a fire (increase in aboveground C:N from 44 to 64 and belowground C:N from 44 to 84).

For Aldous, and analysis of the whole ecosystem response to burning was conducted by simulating 50 years of annual burning and of no burning for a tallgrass ecosystem. We altered aboveground C:N, belowground C:N, and R:S to examine the effect of individual changes in plant physiology on ecosystem function. First we changed individual parameters from default values. The single variable analysis was followed by changes to pairs of parameters, followed by changes to all three variables. Parameters related in inputs and loss from burning were constant for each simulated burn, so that the reported analysis is only indicative of the physiological response to burning. Description of the model and fire impacts on total system response can be found in Ojima et al. (1990). Model calculations of soil organic C, plant production C (both above- and belowground), and net annual N mineralization values were compared to field observations from the Aldous study site.

Results

Immediate response to fire

Soil moisture in the top 5 cm of the burned plots at Aldous and Konza was lower than in the unburned plots, especially during the first two months following the fire. Soil temperatures in top 2 cm of the soil surface of the burned plots were higher relative to the unburned plots at Konza for the first month following the fire. Surface soil temperature maxima of the burned plot were observed to exceed the unburned plot by 20 °C. Combustion losses of aboveground C, N, and P were measured from the 1983 burns. Biomass losses ranged from 3160 at the Aldous plots to 4350 kg/ha at the Konza plots. N losses averaged 25.5 kg/ha at the Aldous plots and 30.0 kg/ha at the Konza plots. P losses were negligible for the burns at either site.

Plant production and soil organic matter

Aboveground live biomass C was 830 ± 340 kg/ha in the burned Konza treatment compared with 410 ± 200 kg/ha in the unburned treatment, after two successive years of burning at Konza. Live root C was also greatly enhanced in the burned treatment, with 1470 ± 390 kg C/ha compared to 820 ± 170 kg C/ha in the unburned (Fig. 1). The N mass contained in live shoots and roots was not significantly influenced by burning. Nitrogen ranged from 6.4–10.4 kg/ha for shoots and 17.3–17.8 kg/ha for roots (Fig. 1).

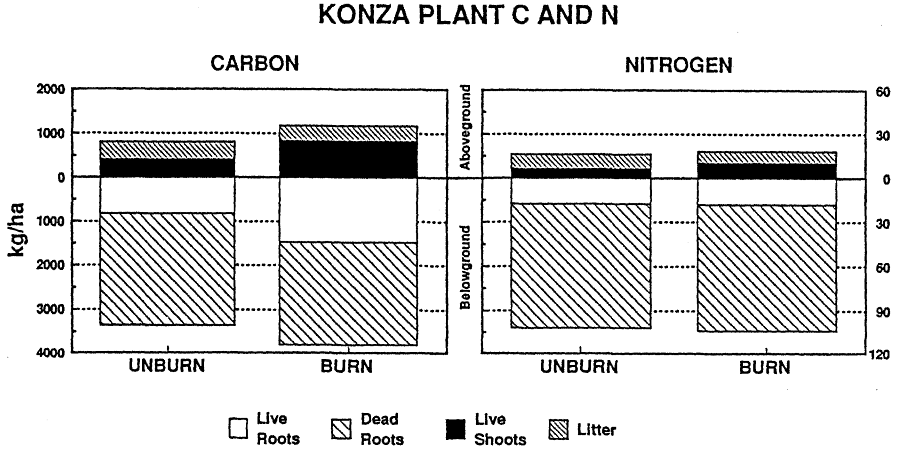

Fig. 1. Aboveground and belowground plant C and N levels at Konza after two years of repeated burning compared to the unburned treatment at Konza. Plots harvested August 1984, values represent a mean of 10 clip plots per treatment for aboveground plant material and a mean of 10 soil cores per treatment to 15 cm depth for belowground plant material. All units are in kilograms per hectare.

Live and dead root C at the annually burned Aldous sites were significantly greater than in unburned Aldous sites (Fig. 2a). In burned plots, live root C was twice that of the unburned, similar to the response at Konza. Dead root C at the annually burned Aldous site was greater than at the unburned site (4500 ± 450 kg/ha vs 2200 ± 340 kg/ha, Aldous burn vs unburned, respectively), but dead root C of the recently burned site at Konza was similar to the unburned sites. Live root N of the annually burned plots at Aldous was the same as live root N from the unburned plots, but dead root N was significantly greater in the Aldous annually burned plots relative to unburned plots. This differed from the response at the recently burned Konza plots, where there was no difference in live or dead root N (Fig. 2b).

Two successive years of burning at Konza resulted in changes in the C:N of roots and shoots. C:N of live shoots on the burn treatment averaged 80 ± 13 compared to 64 ± 5 of the unburned control. Live root C:N of the burned treatment averaged 85 ± 17 compared to 47 ± 15 in the unburned treatment (Fig. 2c). C:N ratios of aboveground litter (dead shoots) also changed after two successive years of burning. Litter C:N in the burned plots were 115 ± 5 compared to 88 ± 8 in the unburned control plots. The C:N of belowground dead material did not change after two years of burning, and values ranged from 27 to 30 at Konza (Fig. 2c). The difference between C:N of burned and unburned sites was larger at Aldous, where annual burning has occurred for over 50 years. Dead roots of the annually burned treatment had a C:N of 44.7 ± 8, whereas, the unburned treatment roots had a C:N of 30 ± 5.

Despite change in root biomass at the Aldous plots, there were small difference between C and N in SOM of the burned and unburned treatments. At the Konza plots, organic carbon in the 0–5 cm layer of both treatments averaged 15 ± 1.2 Mt/ha (Figure 3a) and N averaged 1.5 ± 0.11 Mt/ha (Figure 3b). Organic C in the 5 to 15 cm increment was 2.0 Mt/ha greater in the Konza burned treatment (25 ± 2 Mt/ha vs 23 ± 1.8 Mt/ha, Konza burned vs Konza unburned, respectively); however, N content was not different between treatments at Konza, averaging 2.6 ± 2 Mt/ha. The short period of annual burning (i.e., two years of successive burning) most likely accounts for the small changes in soil C and N storage.

Repeated fires at the Aldous site resulted in lower soil organic carbon in the annually burned plots relative to the unburned controls in the surface 5 cm (12.6 ± 1.3 vs 15.0 ±1.1 Mt/ha, Aldous burned vs Aldous unburned, respectively, Figure 3a). In the 5 to 15 cm soil increment, this difference in organic carbon was reversed (22.8 ± 2.0 vs 19.4 ± 1.8 Mt/ha, Aldous burned vs Aldous unburned, respectively) and over the total 15-cm increment soil C levels were not different between treatments (35.4 vs 34.4 Mt/ha, burned vs unburned, respectively).

Nitrogen mass contained in the surface 5 cm was also lower in the annually burned Aldous plots relative to the unburned Aldous plots (1.0 ± 0.06 vs 1.2 ± 0.08 Mt/ha, burned vs unburned, respectively, Figure 3b). In the next

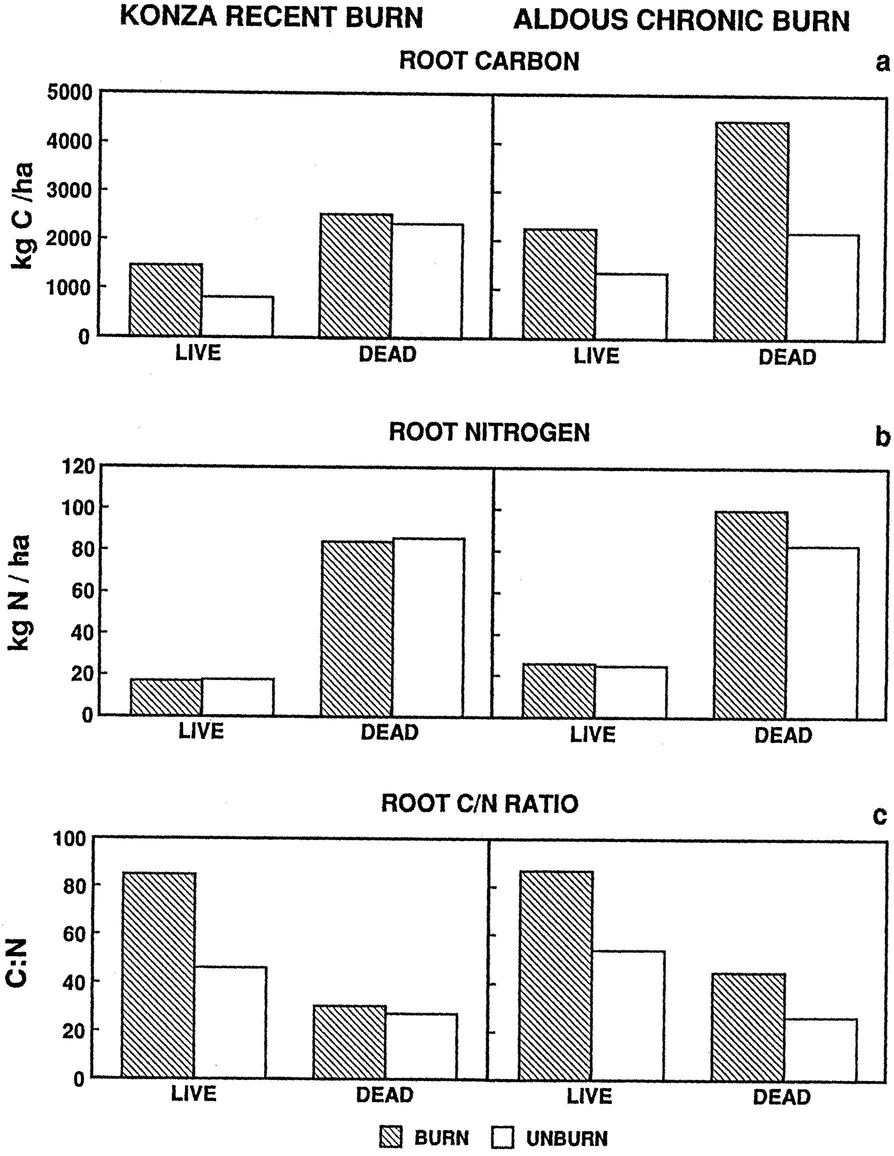

Fig. 2. Live and dead plant roots C, N, and C:N from Konza and Aldous sites. Samples harvested August 1984. All values are means of 10 soil cores taken to 30 cm for each treatment and units are in kilograms per hectare. "*" indicates significant differences at the $p = 0.05$ level.

10-cm increment (5–15 cm depth), there was no difference in the N content in the SOM (1.9 ± 0.1 Mt/ha). Annually burned Aldous plots had a higher C:N in SOM relative to the unburned Aldous plots (12 vs 11, burn vs unburn, respectively).

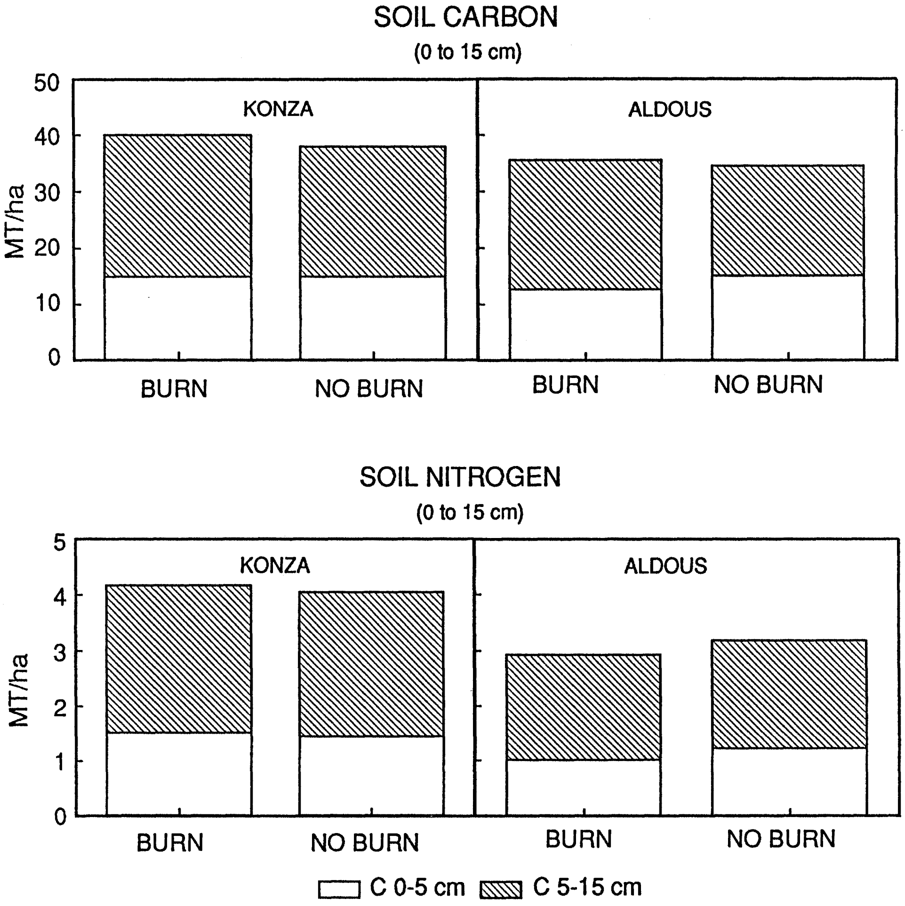

Fig. 3. Soil organic matter content to 15 cm from Aldous and Konza sites. Samples were collected in May 1984. All values are means of 10 soil cores taken in two depth increments, 0 to 5 cm and 5 to 15 cm depth, for each treatment and units are in MT per ha.

Soil nutrients and mineralization

Inorganic N levels were elevated by 7 mg N/kg in burned plots relative to the unburned control immediately following the first burn of the Konza plots. This short-term increase in mineral N at Konza, following the first fire in 20 years, was likely the result of an unusually large release of inorganic N during combustion. This fire caused a deposit in ash of 0.9 kg N/kg, while ash deposits at the annually burned Aldous sites were typically 0.2 kg/ha. After the initial release of N from ash at Konza, available N (NO_3^- and NH_4^+) of unburned plots at both Konza or Aldous was typically 5 to 10 mg N/kg higher than in the burned plots.

Net N mineralization rates of the surface 5 cm were significantly lower in the annually burned plots at Aldous than the unburned Aldous treatment (Table 1). Net N mineralization was approximately 7 kg N/ha in the Aldous burn plots (Over 120 d between May and August) compared to 11–26 kg N/ha at Konza or the Aldous unburned plots. The net N mineralization rate of the unburned Aldous plots was the highest of all treatments in both absolute rates and relative to SOM C or N. The burned and unburned sites at Konza did not show significant differences in net N mineralization for the growing season, May through August, in either 1983 or 1984.

The soil transfer experiment resulted in a decreased net N mineralization of soils transferred to unburned plots, whereas those transferred to burned plots had increased net N mineralization. The reduction in net N mineralization ranged from 3.0 kg N/ha (Aldous burn 1984, Table 1) to 14.0 kg N/ha (Konza burn 1983). The average reduction in net N mineralization of burn

Table 1. Field estimates of cumulative net N mineralization for 120 d field incubation at Konza and Aldous in the surface 5 cm of soil. Cumulative net N mineralization and cumulative net N mineralization per unit soil N for burned and unburned treatments are presented. Difference between mineralization of transferred soil and in situ soil incubations are indicated in the last column, negative values indicate lower N mineralization in the transferred soil incubation.

Site treatment	In situ N min. 120 d (kg/ha) (± s.e.)	N Min./Soil N (%) (± s.e.)	Difference (Transfer – in situ) (kg/ha)
1983			
Aldous			
Burn	7.1**	0.59**	–6.6‡
	(1.7)	(0.15)	
Unburn	26.5	1.72	15.4‡
	(2.7)	(0.21)	
Konza			
Burn	15.3	0.91	–14.0‡
	(3.7)	(0.23)	
Unburn	11.4	0.70	2.2
	(1.9)	(0.12)	
1984			
Aldous			
Burn	7.3**	0.51**	–3.0†
	(1.9)	(0.16)	
Unburn	20.9	1.23	5.0†
	(2.5)	(0.19)	
Konza			
Burn	12.9	0.63	–4.8†
	(2.2)	(0.11)	
Unburn	12.2	0.66	1.6
	(2.6)	(0.16)	

** Treatment within a site are significantly different ($p < 0.05$), $n = 8$.
† Designates significance at the 0.10 level.
‡ Designates significance at the 0.05 level.

treatment soils incubated in unburned plots was 7.1 kg N/ha. When transfers were made in the opposite direction (e.g., unburn soil incubated in burned plots), net N mineralization increased at Aldous (5.0 kg N/ha in 1984 to 15.4 kg N/ha in 1983); however, no differences in net N mineralization were observed at the Konza treatments between transfers from unburned to burned plots.

Burning for one or two years at Konza resulted in a slight but significant increase in microbial biomass C but not in microbial N (Table 2). Microbial biomass C and N was significantly lower in the long-term annually burned plots at Aldous than in the unburned Aldous plots. Microbial biomass C:N were significantly wider in the Konza and Aldous burned plots than in the respective unburned plots (Table 2).

Table 2. Microbial biomass C and N for Aldous and Konza burned and unburned treatments in the surface 5 cm of soil. Values are averages of 8 samples periods collected over the 1983 and 1984 field seasons.

Site treatment	Microbial biomass C (kg C/ha)	Microbial biomass N (kg N/ha)	Microbial C/N Ratio	K_n	Microbial C/Soil C (%)	Microbial C/Soil N (%)
Aldous						
Burn	795**	132**	6.01**	0.25**	5.64	66.4**
Unburn	895	153	5.86	0.30	5.40	58.2
Konza						
Burn	1080**	182	5.93**	0.31	6.32	63.8
Unburn	1030	177	5.78	0.32	6.19	63.3

** Treatments within a site are significantly different ($p < 0.05$).

The proportion of microbial biomass N mineralized following chloroform incubation (K_n) was significantly lower at the Aldous burned plots (Table 2), 0.25 compared to 0.30 of the Aldous unburned plots. The Konza burned and unburned plots showed no significant change. The lower K_n value and the significantly wider C:N of the microbial biomass of the Aldous burn suggest that a change in microbial composition has occurred as a result of prolonged annual burning.

Soil organic matter quality

Laboratory estimates of N mineralization potential and soil respiration (Cr) were made to determine the quality and immobilization potential of SOM (Table 3). Soils from the Aldous site respired less CO_2 than soils from the Konza site. Overall, burning had little effect on the amount of C respired during the 70-d incubation from soils collected at either Konza or Aldous sites.

Net N mineralization rates from the 70-d incubations ranged from 22.4 to

Table 3. Soil respiration and N mineralization potential for burned and unburned treatments at Konza and Aldous for 1984 in the surface 5 cm. All values based on cumulative 70 d laboratory incubations. Incubations were conducted under uniform temperatures (25 °C ± 1°) with 100% humidity in the dark. Values are an average of 10 samples per treatment.

Site treatment	Soil respiration (C_r) (kg/ha)	Net N mineralization (N Min.) (kg/ha)	C_r/ N Min.	C_r/ Soil C (%)	N Min./ Soil N (%)	N Min./ Microbial N (%)
Aldous						
Burn	695	22.4**	36.0**	4.92	1.87**	15.5**
Unburn	715	37.8	20.9	4.31	2.31	22.7
Konza						
Burn	810	39.5**	22.1	4.13**	2.33*	22.5**
Unburn	830	34.5	24.5	5.01	2.12	19.5

** Treatments within a site are significantly different ($p < 0.05$).

39.5 kg N/ha (Table 3). Unburned soils from both Konza and Aldous showed similar amounts of mineralized N (35 and 38 kg N/ha, respectively). The burned soils varied greatly in their mineralized N content. Burned soils from Aldous mineralized 22 kg N/ha (averaged over all sampling dates), and burned soils from Konza mineralized approximately 1.5 times more than the Aldous burn soils (Table 3).

The ratio of respired CO_2 to mineralized N has been used as an indicator of substrate quality and immobilization potential (Schimel et al. 1985). Over the short-term (2 years of annual burning), burning had no significant effect on the ratio of CO_2 respired to net N mineralized (Table 3). The long-term effect (over 30 years of annual burning) of burning caused a significant increase in the ratio, suggesting more immobilization due to lower substrate quality or larger substrate quantity in long-term burned areas.

Model evaluation of the plant physiological consequences of burning

When fire was simulated with no physiological feedbacks to change the C:N of above- or belowground plant parts or the R:S, the simulated results did not reflect the observed trends of this field study, in that soil C losses and net annual N mineralization rates were overestimated and belowground production was underestimated (Table 4). Modifying C:N and R:S individually did not markedly improve the overall fit to the field data, although changes in C:N did improve the prediction of some ecosystem properties. For example, changing aboveground C:N improved the prediction of aboveground plant production, but resulted in lower values for soil C and root production that those observed in the field, and simulated N mineralization rates did not resemble the observed differences between burned and unburned treatments at Aldous. Changes in belowground C:N resulted in better predictions of

Table 4. Fire impact on biological feedback through changes in nitrogen use efficiency and root-to-shoot allocation using CENTURY model simulations.

Treatment	Soil carbon top 20 cm ($g \cdot m^{-2}$)	Above plant production ($g\ C \cdot m^{-2} \cdot y^{-1}$)	Below plant production ($g\ C \cdot m^{-2} \cdot y^{-1}$)	Net N mineralization ($g\ N \cdot m^{-2} \cdot y^{-1}$)
No burn	4880	144	164	4.6
Fire no feedback	4100	153	174	4.4
Fire AG NUE	4260	166	189	4.3
Fire BG NUE	4270	163	185	3.4
Fire root/shoot	4240	131	202	4.6
Fire AG/RS	4370	140	216	4.5
Fire BG/RS	4450	141	217	3.4
Fire AG/BG/RS	4620	152	235	3.2

treatment differences in net N mineralization and aboveground plant production, yet still did not simulate adequate soil C or root production relative to observed data (Table 4).

The combined modification of belowground C:N and R:S resulted in a good prediction of aboveground and root production and net N mineralization; however, the simulation slightly underestimated soil C levels. The best simulation of the whole ecosystem response to long-term burning resulted from changing all three factors (above-and belowground C:N and R:S). Fire impacts several components of the tallgrass ecosystem: so single factor studies may only reveal partial or misleading views of causation in the total ecosystem response to fire. Physiological feedbacks of the tallgrass plants are important factors in sustaining the tallgrass prairie over long periods of annual burning.

Discussion

Our study focused on internal biogeochemical dynamics of tallgrass prairie in response to fire, but it must be remembered that the biogeochemistry of fire in prairies is also influenced by interactions with grazing (Hobbs et al. 1991). Grazing reduces overall N losses due to burning by about 50%, and at that level, atmospheric inputs balance or nearly balance combustion losses (Hobbs et al. 1991). Here, we present a detailed study of internal readjustments of biogeochemical cycling as a result of changes in plant allocation of C and N in the absence of grazing.

The apparent effect of burning on plant production in the tallgrass prairie does not entirely result from improved N availability, as suggested by other studies (Sharrow & Wright 1977; Woodmansee & Wallach 1981). The increase in productivity results from modifications of site biophysical properties due to the removal of aboveground litter and from changes in plant physiological responses. Hulbert (1988) concluded that fire removal of the litter layer and the subsequent heating of the soil early in the growing season, when adequate soil moisture is available, is a major contributing factor in the enhanced plant, production after burning. Litter removal resulted in greater photosynthetic capacity of the dominant tallgrass species, including *Andropogon gerardii* and *Sorgastrum nutans* (Weaver & Rowland 1952, Knapp 1984, 1985). Knapp (1984) concluded that increased photosynthetically active radiation (PAR), resulting from litter removal, was the most significant factor contributing to the enhanced plant growth.

These biophysical factors (i.e., increased soil temperature and PAR) all contributed to physiological modifications, greater photosynthetic capacity and higher nitrogen use efficiency (NUE, i.e., greater C gained per unit N utilized), leading to enhanced production in the burned tallgrass prairie. Changes in the NUE of tallgrass prairie plants due to enhanced photosynthesis and warmer root temperatures result in changes in soil organic matter turnover and N cycling patterns. Greater than 50% of the organic matter inputs come from belowground inputs in tallgrass prairie soils (Kucera & Dahlman 1968; Seastedt 1988). Wedin & Tilman (1990) observed more than 4 times as much belowground litter production as aboveground litter production in newly seeded grass plots. A higher C:N in live roots was a relatively rapid change that persisted with repeated burning, as it was observed after two years of burning at Konza and after 50 y at Aldous. In the long-term burned plots (Aldous), it was also observed in dead roots. Dead roots with a wide C:N immobilize large amounts of N during decomposition (Holland & Detling 1990). Fire enhances the production of lower quality root material, thereby enhancing root N immobilization. Changes in litter quality can result in a positive feedback whereby plants that have a high NUE may promote conditions of low nutrient availability, giving an advantage to plants that have a high NUE (Vitousek 1982; Chapin et al. 1986). Enhanced belowground production following fire, and associated inputs of plant material with higher C:N resulted in lower net N mineralization, despite the warmer soils and possibly higher gross N mineralization.

These changes in NUE and C allocation are critical to nutrient and community dynamics of the tallgrass prairie ecosystem. In a recent study by Wedin & Tilman (1990), C_4 prairie grasses, including *Andropogon gerardii*, were seeded into monospecific plots. They observed that the C_4 grasses produced biomass at a low investment of N (i.e., high NUE) and allocated most of their biomass belowground. A marked reduction in the amount of available soil N relative to C_3 monocultures was also observed (Tilman & Wedin 1991). The C_4 grasses produced litter of lower quality (e.g., higher lignin content, lower N concentration and higher C:N), especially belowground (Wedin & Tilman 1990; Tilman & Wedin 1991) and promoted conditions that allow for a slow release of N. Their results suggest that nutrient competition is controlled by the ability of C_4 species to maintain low levels of N in the soil solution while still maintaining high levels of productivity (Tilman 1990). A positive feedback is developed that promotes low N concentrations in the soil solution, favoring C_4 grasses with high NUE. These plants produce litter with high C:N, which tends to immobilize N maintaining low nutrient availability.

Fire in the tallgrass ecosystem seems to enhance the feedback on NUE, providing a mechanism by which C_4 tallgrass species with high NUE, can persist despite recurrent fires and loss of soil N. So counter to enhancing N availability, burning reduces N availability and may increase plant demand through improved growing conditions (Schimel et al. 1991). This effect on N availability following burning is consistent with fertilization studies where tallgrass prairie grasses positively responded to N additions (Rains et al. 1975; Seastedt et al. 1991). This fertilizer response is reversed following several years of fire suppression, indicating that the demand for N is being adequately met under these conditions. Without a fire, a build-up of the surface litter slows the decomposition of soil organic matter resulting in greater soil organic matter C and N. This eventually leads to higher levels of soil solution N (Seastedt & Ramundo 1990) due to lower uptake efficiency of the plants and greater SOM-N, which in time allows for the competitive advantage to shift toward C_3 species (Towne & Owensby 1984).

In summary, our initial hypotheses underestimated the role of the increased plant allocation belowground after fire and the overall impact that fire had on plant production through changes in NUE. The significant change in NUE, especially belowground, and higher R:S maintained plant C inputs to the soil system despite combustion losses of the aboveground plant material. This modification of plant production following a fire resulted in changes in plant residue quality that affected N mineralization rates and soil organic matter dynamics. Rates of N mineralization following burning in these systems did not show the predicted increase due to the countervailing effects of higher C:N of belowground inputs. The input of lower quality material resulted in greater immobilization of N in soil. Overall, plant production following long-term annual burning was maintained because of increased NUE but not higher N availability. Soil organic matter was maintained by the input of belowground plant material. These biological feedbacks following a fire in the tallgrass ecosystem provide a plausible explanation for the continued long-term productivity of annually burned systems, despite nutrient losses.

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